

# Habitat and Ant-Attendance in Hemiptera : a Phylogenetic Test with Emphasis on Trophobiosis in Fulgoromorpha

*Thierry BOURGOIN*

E.P. 90 CNRS, Laboratoire d'Entomologie, Muséum national d'Histoire naturelle,  
45, rue Buffon, 75005 Paris, France

## ABSTRACT

The biological attribute "ant-mutualism" is so widely distributed within the Hemiptera that SCHAEFER (1987) suggested that the association of Hemiptera with ants represents the retention of an early way of life which originated on the ground and always preceded a life up on plants. A phylogenetic test of SCHAEFER'S scenario indicates that ant-mutualism cannot be retained as ancestral for all major hemipteran clades but arose independently several times in groups for which habitat is above ground. Causation between a ground habitat and ant-attendance is not corroborated. Special attention is paid to trophobiosis in Fulgoromorpha. Although all planthoppers could theoretically be associated with ants only a few of them are ant-attended, and mainly the Tettigometridae. Members of this family share morphological characteristics (no jumping apparatus, no wax plates, no sensory pits, a long anal tube, no anal combs, no anal apodemes in adults) and particular fulgoromorph behavior traits (subsociability, sessile behavior) that could have evolved under selection for trophobiosis. This calls for a reanalysis of these morphological and behavioral characters that have been generally considered as plesiomorphic. Durable fulgoromorph-an ant associations are observed when planthoppers are unable to escape or live with gregarious or subsocial behaviors.

## RÉSUMÉ

### **Habitat et relations avec les fourmis chez les Hémiptères (plus particulièrement les Fulgoromorphes) : un test phylogénétique.**

L'attribut « mutualisme avec les fourmis » a été si souvent observé chez les Hémiptères que SCHAEFER (1987) a suggéré que l'association Hémiptères-fourmis serait l'expression d'un mode de vie ancestral ayant pris place au niveau du sol avant que ces insectes ne conquièrent les strates supérieures de la végétation. Un test phylogénétique réfute le scénario de SCHAEFER et montre que le mutualisme avec les fourmis ne peut être retenu comme un état ancestral pour tous les grands clades d'Hémiptères. Au contraire, il serait apparu de manière indépendante à plusieurs reprises chez des groupes occupant déjà une strate de végétation supérieure. La relation de causalité entre vie au niveau du sol et mutualisme avec les fourmis n'est donc pas retenue. La trophobiose chez les Fulgoromorpha est plus particulièrement abordée. Bien que théoriquement tous les Fulgoromorphes puissent maintenir des relations trophobiotiques avec les fourmis, seules quelques espèces sont concernées, et tout particulièrement les Tettigometridae. Cette famille présente des caractéristiques morphologiques (pas d'appareil de saut, pas de plaques cirières ni de fossettes sensorielles, un tube anal allongé, absences des processus pectinés et des apodèmes anaux chez l'adulte) et éthologiques (comportements subsocial et faible mobilité) qui auraient pu être sélectionnées dans le contexte du comportement de trophobiose. Ceci plaide pour une nouvelle étude de ces caractères morphologiques et appelle à vérifier leur homologie primaire supposée avec les états plésiomorphes observés chez les Cicadomorphes. Seuls les

Fulgoromorphes qui sont subsociaux et/ou ne peuvent s'éloigner des fourmis semblent présenter des associations durables avec les fourmis.

## INTRODUCTION

One of the major problems in evolutionary biology is the impossibility of repeating speciation experiment. Evolution is a historical process with a unique result, and the repetition of an experiment which validates the scientific results is inapplicable in this field of study. Evolutionary biologists thus have substituted for the repetition of experiment the repetition of observation. How those observations are organized and studied are the object of comparative biology, the purpose of which is a better understanding of "the extent and pattern of organic diversity" (HUEY, 1987).

Until the last two decades, diversity of a biological trait was most often analyzed according to a "horizontal analysis": the different states of the trait were observed and a scenario was inferred according to an *a priori* general idea of evolution of the group. In such a view the proposed scenario took into account at the same time the observed states of the trait (pattern), the mechanisms which select the trait and those involved for its maintenance (processes) and it was impossible to distinguish between them. Patterns and processes were merged in the same explanation. Since then, one has seen increasing concern of taking into account the historical dimension in comparative biology. Analysis of the diversity of a biological trait has now to be rooted in the phylogeny according to a "vertical analysis". The result of this has been the shift from empirical methods to analyze a biological trait to more formalized ones. The former were producing a "series of natural histories" incorporating *ad hoc* explanations which were difficult to evaluate. The latter now result in refutable "evolutionary scenarios" directly linked with phylogenetic patterns (FUNKS & BROOKS, 1990; BROOKS & MCLENNAN, 1991; ...).

To study and compare biological traits (morphological, physiological, behavioral or ecological) between different taxa, two main types of methodologies have been developed. The first uses statistical techniques (RIDLEY, 1989; FELSENSTEIN, 1985; HARVEY & PAGEL, 1991...); the second consists of mapping the traits being studied onto cladograms (CODDINGTON, 1988; BROOKS & MCLENNAN, 1991; GRANDCOLAS *et al.*, 1994; ANDERSEN, 1995; ...). In this last case, patterns of biological traits are produced and used to test proposed models of evolutionary processes. If the model fits the pattern observed then it is corroborated. Indeed, such procedures do not aim to explain how evolution has proceeded (processes) but seek to describe or to account for what has happened (patterns). Patterns and processes provide each by themselves a better understanding of evolution but any explanation by processes using models needs to fit with what has happened as it is shown by patterns. In such a way, phylogenetic patterns test evolutionary scenarios proposed by models or allow one to infer new evolutionary scenarios waiting for models (ELDRIDGE & CRACRAFT, 1980; CARPENTER, 1989; GRANDCOLAS *et al.*, 1994). All these methodologies provide new insights into the origin and the development of biological traits and more generally they are concerned with the origin and the development of biodiversity. Revisiting old well-established ideas using these new approaches has most often raised new and sometimes unexpected interpretations about different aspects of evolution: *e.g.* cave adaptation and return to epigeal life, (DESUTTER-GRANDCOLAS, 1994) or social behavior and return a solitary way of life (PACKER, 1991).

With special attention paid to the Auchenorrhyncha and the Fulgoromorpha within the Hemiptera, the first aim of this paper is to revisit the interpretation of causation (GRANDCOLAS *et al.*, 1994) given for two biological attributes (*sensu* MICKEVICH and WELLER, 1990): “habitat” and “ant-attendance”. Ant-attendance, or trophobiosis, is so widely distributed within the Hemiptera that SCHAEFER (1987) has suggested that the association of Auchenorrhyncha with ants represents the retention of an early way of life and is “a secondary consequence” of the ancestral habitat (ground level) of the Auchenorrhyncha (SCHAEFER, 1981, 1987). The second aim of this work is to provide the basis for new research directions on ant-fulgoromorph mutualism with special attention paid to the Tettigometridae on both morphological and behavioral particularities of this family.

## MATERIALS AND METHODS

### Methodology

Both “habitat” and “trophobiosis” are two traits for which homology is difficult to establish. They cannot be directly used in constructing phylogenies where an hypothesis of primary homology has to be proposed first for the putative synapomorphies (DE PINNA, 1991). They are used here as “attributes”, according to the meaning of MICKEVICH and WELLER (1990). The mapping methodology has been used in this work. All trait states are unordered and Wagner parsimony (FARRIS, 1970) is used to optimize them onto the cladogram using MacClade, version 3.06, (MADDISON and MADDISON, 1992).

To test if there is any relation between the habitat and its changes and evolution of trophobiosis in the focal group, the following protocol was employed:

1. Mapping the different habitats observed onto a phylogeny (DELEPORTE, 1993) and inferring historical changes to determine the ancestral state.
2. Mapping trophobiosis onto the same phylogeny and inferring the ancestral state of this attribute.
3. Inferring from the changes observed at the different nodes how the two attributes, “ant-attendance” and “habitat”, are linked onto the cladogram and whether there is any indication of causation or relationship (GRANDCOLAS *et al.*, 1994) between the two traits.

### Phylogenetic background

Hemipteran and Fulgoromorphan phylogenies have been widely recast in the last few years and differ substantially from the classic view summarized by EVANS (1963, 1977) and used by SCHAEFER (1987). This results from recent phylogenetic works dealing with morphological (ASCHE, 1988; EMELJANOV, 1987, 1990; DIETRICH & DEITZ, 1993; BOURGOIN, 1993b) and/or molecular data (WHEELER *et al.*, 1993; SORENSEN *et al.*, 1995; CAMPBELL *et al.*, 1994, 1995; VON DOHLEN and MORAN, 1995; BOURGOIN *et al.*, 1997). Homoptera is no longer considered as a monophyletic group (SORENSEN *et al.*, 1995) and even the monophyly of the Auchenorrhyncha is now questionable (BOURGOIN, 1993b; CAMPBELL *et al.*, 1995). Within Fulgoromorpha, the basal position of the Tettigometridae has been recently debated: morphological and molecular evidence now places this clade among more recent lineages (BOURGOIN *et al.*, 1997). The classical (*e.g.* SCHAEFER, 1987) and the revised (represented by the consensus of these recent cladistic analyses) Hemiptera and Fulgoromorpha phylogenies have been both tested in this study. According to SORENSEN *et al.* (1995), Euhemiptera refers to the monophyletic group [Cicadomorpha + Neohemiptera] and Neohemiptera to [Fulgoromorpha + Coleorrhyncha + Heteroptera].

### Attributes: habitat and ant-attendance

The different states of the attributes “habitat” and “ant-attendance” for the major taxa of Hemiptera and for the Cicadomorpha and Fulgoromorpha families are provided in Table 1. Nymphal habits, when known, have been chosen first to determine the state of the habitat attribute in the different lineages. This assumes that nymphs retain more specific information (“more conservative”, SCHAEFER, 1987) than adults which are more likely to expand their habitat and their range of host plants as also noted by WILSON *et al.* (1994). Most information comes from SCHAEFER (1987) with some modifications. Data have been completed mainly for the Fulgoromorpha using WILSON *et al.*'s (1994) important paper for the habitat. For Tettigometridae, it has been reported several times that they have been found underground attended by ants. This has led to the idea that “tettigometrid nymphs typically live on plant roots” (EMELJANOV, 1987), a view that has been widely accepted (O'BRIEN & WILSON, 1985; WILSON *et al.*, 1994) although, in fact, most nymph and adult tettigometrids live on and more generally above ground (most Hildinae and Egropinae, many Tettigometrinae, BOURGOIN, unpublished data). Therefore tettigometrid habitat has been coded as polymorphic. Even if some cercopoid nymphs are well known to occur in masses of froth on low grasses or in fluid-filled tubes (Machaerotidae), such behavior is most probably derived (BOULARD, 1991). According to MAA (1963) and SCHAEFER (1987), Cercopoidea are considered as originally subterranean (many cercopoid and

aphrophorid nymphs) as Cicadoidea nymphs. Heteroptera and Coleorrhyncha are considered to live on the ground (SCHAEFER, 1981; SCHUH & SLATER, 1995), whereas habitat of Sternorrhyncha as above ground (FOLDI, REMAUDIERE, pers. com., and FOLDI, 1997 in this volume).

Trophobiosis in Auchenorrhyncha is documented by DIETRICH & MCKAMEY (1990), BUCKLEY *et al.* (1990), ROZARIO *et al.* (1992, 1993). In Cicadellidae, ant-leafhopper mutualism is rare and scattered among several subfamilies.

TABLE 1. — General habitat and ant-attendance in major Auchenorrhyncha taxa. Data sources in text.

Taxa	Habitat	Ant-attendance
Sternorrhyncha	above ground	not in basal groups
Cicadomorpha:		
Aetalionidae	above ground	+
Cercopoidea	in or on ground	-
Cicadoidea	in ground	-
Cicadellidae (other)	above ground	-
Eurymelinae	in, on or above ground	some species
Macropsinae	above ground	some species
Melizoderidae	?	?
Membracidae	above ground	+
Fulgoromorpha:		
Achilidae + Achilixiidae	above ground, under bark	-
Cixiidae	in ground	some species, in ant nests
Delphacidae Ugyopini	on ground (plant crown)	-
Delphacidae Asiracini	on ground (plant crown)	-
Delphacidae (other)	on ground (plant crown)	some species, under ant shelters
Derbidae	above ground, under bark	-
Dictyopharidae	above ground	-
Eurybrachidae	above ground	-
Flatidae	above ground	-
Fulgoridae	above ground	-
Gengidae	?	?
Hypothonellidae	in ground	in ant nests
Issidae + Acanaloniidae	above ground	some species
Kinnaridae + Meenoplidae	in ground (kinnarids)	-
Lophopidae	above ground	-
Nogodinidae	above ground	-
Ricaniidae	above ground	-
Tettigometridae	in, on or most often above ground	most often outside ant nests
Tropiduchidae	above ground	-
Coleorrhyncha	on ground	-
Heteroptera	on ground	not in basal groups

DIETRICH & MCKAMEY (1990), reporting the cases already known, have shown that although most of the species in which ant-mutualism occurs belong to subfamilies generally thought to be old lineages (NIELSON, 1985), their apparent taxonomic disjunctions among Cicadellidae suggests multiple origins of these behaviors. Indeed, several cases of ant-mutualism are reported in euryeline and macropsine leafhoppers which are considered to have a relative basal place in the Cicadellidae phylogeny. This information has been incorporated into the study by including a polymorphic status for these two taxa in regard to ant-attendance. The other Cicadellidae subfamilies (Agallinae, Iassininae, Hecalinae, Idiocerinae), in which only one or two cases of ant-attendance have been reported, are not included in this study. Excepted for Tettigometridae, trophobiosis in Fulgoromorpha is poorly documented (see further the second part of this study) and also scattered among different families. Treating ant-attendance as a polymorphic attribute has been used for the Fulgoromorpha Cixiidae, Delphacidae and Issidae. In Delphacidae where the phylogeny is best known the first divisions Ugyopini and Asiracini (*sensu* ASCHE, 1990, but see Emeljanov, 1995) have been used. Trophobiosis in Sternorrhyncha and Heteroptera is restricted to non basal taxa (Sternorrhyncha and Heteroptera phylogenies according to CAMPBELL *et al.* (1994) and WHEELER *et al.* (1993) respectively) and thus without incidence possible on the ancestral state of this attribute which then has been considered as absent for these groups in this study.

## RESULTS AND DISCUSSION

### *Habitat*

Mapping the attribute habitat onto the revised phylogeny (Fig. 1) leads to an equivocal result for the Hemiptera and the three states in, on or above ground are equally parsimonious (7 steps each). Moreover, one cannot propose any ancestral state for the Euhemiptera, the Cicadomorpha, the Neohemiptera or the Fulgoromorpha. In order to try to resolve these equivocal results and because the sister group of the Hemiptera is still unclear (KRISTENSEN, 1995), a basal group to the Hemiptera has been added permitting a test of the three different attribute states (Fig. 2, test 1, 2, 3). All trees are equal with a five step length. An "above ground" basal state does not resolve the equivocal results (Fig. 2a). An "on ground" basal state provides a full resolution: the ancestral state for the Euhemiptera, the Neohemiptera and the Fulgoromorpha is "on ground", while it is in ground for the Cicadomorpha (Fig. 2b). With an "in ground" basal state, the Neohemiptera and the Fulgoromorpha are left with an equivocal result between on or in ground, while the ancestral state for Cicadomorpha remains "in ground" (Fig. 2c).

The putative sister groups for the Hemiptera are either the [Psocodea + Thysanoptera] or the Thysanoptera alone (KRISTENSEN, 1995). Insects in these two lineages live generally on ground (Psocodea, Terebrantia) but some live also above ground. This last state does not allow to resolve the equivocal results. If one retains an ancestral state on the ground for the Hemiptera, there is no equivocal result and one can suggest the following evolutionary scenario for the changes of habitat (Fig. 2b). The ancestral habitat state for the Hemiptera was probably on ground and each major lineage has evolved in its own direction, whether above ground in Sternorrhyncha, in ground in Cicadomorpha (nymphs) or on ground in Neohemiptera. In Cicadomorpha, the Membracoidea (*sensu* DIETRICH & DEITZ, 1993) have evolved to an above ground habitat for all instars. In Fulgoromorpha one lineage (Delphacidae, Cixiidae, Kinnaridae-Meenoplidae) has moved to an underground habitat (Cixiidae and Kinnaridae-Meenoplidae nymphs) and a second lineage has changed to a complete above ground life. This evolutionary scenario agrees with EMELJANOV (1987) rather than WILSON *et al.* (1994) who retain an ancestral subterranean feeding for the Fulgoromorpha and Auchenorrhyncha as a whole.

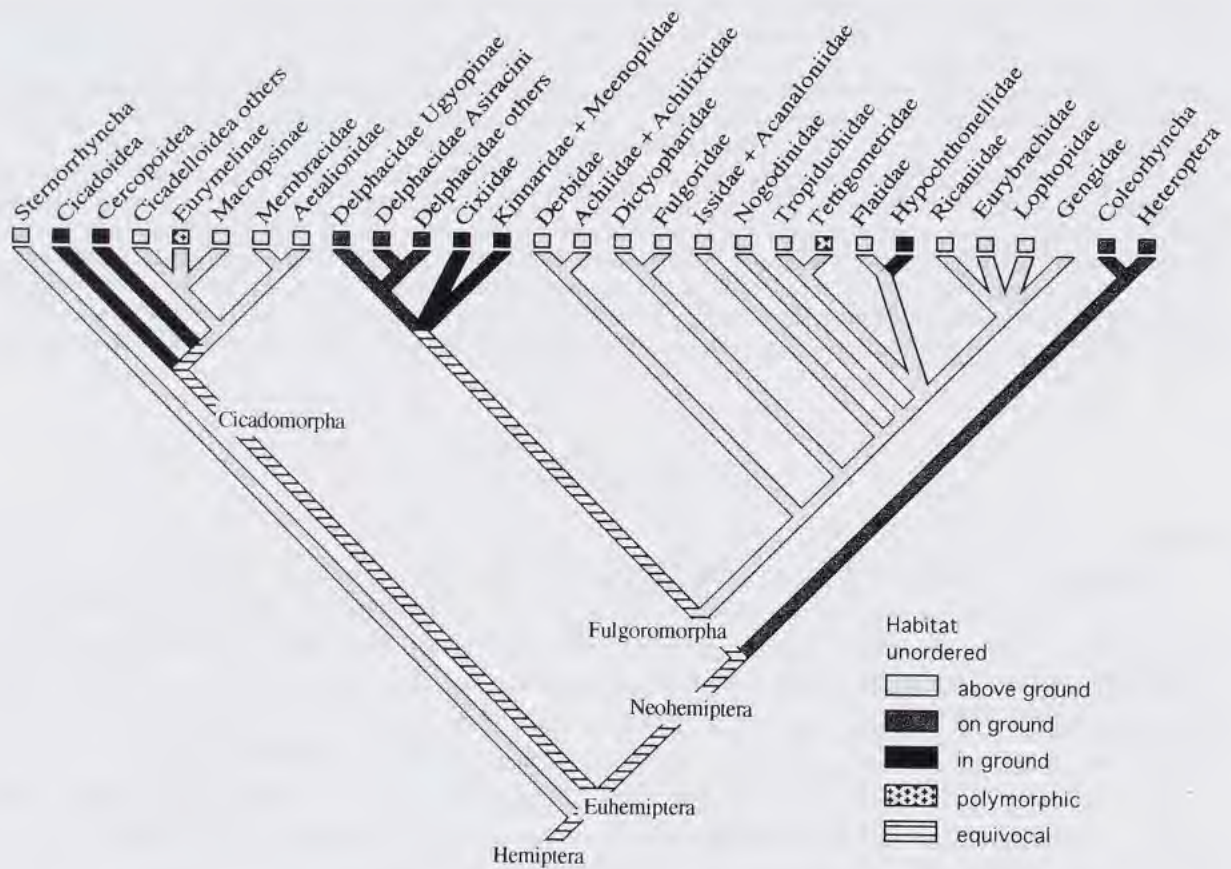


FIG. 1. — Optimization of the habitat attribute (in, on or above ground) upon the phylogeny of the Hemiptera.

### *Ant-attendance*

The ancestral state of this attribute corresponds to an absence of ant-attendance for all the major lineages: Hemiptera, Cicadomorpha, Euhemiptera, Neohemiptera and Fulgoromorpha (Fig. 3). Within these clades each subgroup exhibiting trophobiosis has acquired this behavior independently except for the clade Aetalionidae + Membracidae. This last result needs however to be confirmed. Several taxa of membracids are known to be unattended by ants and an ancestral trophobiosis condition in Membracidae may not be retained if these taxa are confirmed as basal taxa. Indeed, recent results of DIETRICH & DEITZ's (1993) phylogeny combined with WOOD's observations (1984) show for instance that Stegaspidini in the basal Stegaspidinae are unattended. Ant-attendance in Fulgoromorpha is scattered throughout the taxa.

### *SCHAEFER's scenario*

SCHAEFER (1981) suggested that the original habitat of Hemiptera was on the ground. He considered that, from a ground-dwelling hemipteran ancestors, two basic stocks emerged. One became predacious and developed into the Heteroptera; the other lineage became phytophagous,

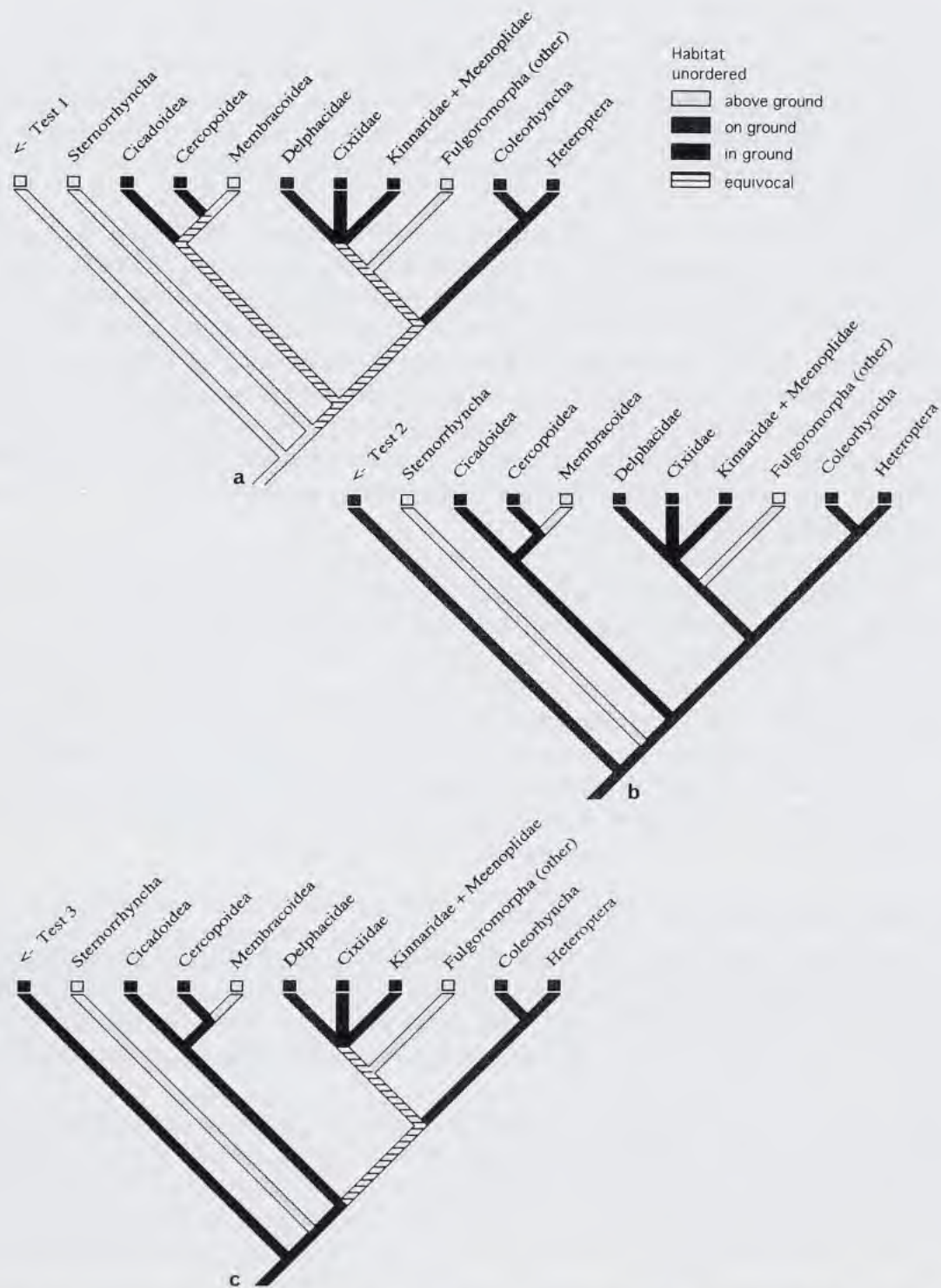


FIG. 2. — Tests for optimization of the habitat attribute upon the phylogeny of Hemiptera inferring each habitat state possible at the base of the tree. Each cladogram is equally parsimonious to the others but only one (Test 2) allows a non equivocal resolution for this attribute. a: Test 1: above ground; b: Test 2: on ground; c: Test 3: in ground.

sucking plant juices (probably from roots), and developed into the Homoptera (SCHAEFER, 1987). As many members of the Hemiptera, "... especially many evolutionarily older members, live in ground debris, or on just below the surface of the ground, or associated with ground biota (such as roots, ants, burrowing mammals), or in groundlike habitats (e.g. in nests, under bark)", this type of habitat "represents the retention of an early way of life; [...] it is probable that the association with ants originated on the ground, and always preceded a life up on plants" (SCHAEFER, 1987).

SCHAEFER's scenario is thus built on three successive steps: 1. Hemiptera lived ancestrally on the ground, 2. Ant attendance was an ancestral attribute for Auchenorrhyncha, and 3. Ant attendance preceded change of habitat from in/on ground to above ground. However the last two steps are refuted and ant-attendance has appeared several times independently after all clades have moved above ground. Indeed and according to the phylogeny used by SCHAEFER (Fig. 4), mapping and optimizing parsimoniously the different types of habitat observed shows that it is impossible to decide if the state in, on or above ground (9 steps each) represents the ancestral state in the Hemiptera. For the second attribute the ancestral state corresponds to an absence of ant-attendance for all the major lineages: Hemiptera, Auchenorrhyncha, Cicadomorpha, Neohemiptera, Fulgoromorpha.

Why do we obtain different results? To address this scenario SCHAEFER has clearly tried to link his argument with the historical perspective according to three main points. The first one is in accordance with the methodology used here: the phylogenetic pattern allows one to choose between plesio-apomorphic states of the character under study using a parsimonious optimization. However SCHAEFER has added two more points to build his scenario: "ingroup commonality criterion" and "older characters are primitive". Unfortunately, these criteria are well known to be inappropriate and should not be used to address character polarity (HENNIG, 1966; NELSON & PLATNICK, 1981; WATROUS & WHEELER, 1981; and reviews in BROOKS & MACLENNAN, 1991 or FOREY *et al.*, 1992). Using these criteria and adding *ad hoc* hypotheses lead to build a scenario out from parsimony and to rend it unrefutable.

#### *Ant-attendance and habitat in the Hemiptera*

In conclusion, which scenarios can be proposed for these two attributes according to the above analyses? A parsimonious account of the patterns observed for these two attributes is proposed here with some *hypotheses* on the processes which could have been involved to explain these patterns. These are not *ad hoc* arguments but just possible explanations that still need to be tested.

With SCHAEFER (1987) one can retain a ground level habitat as an ancestral condition in the Hemiptera as a whole. One may expect that for competitive reasons (?) each major lineage has evolved by itself either on ground (Neohemiptera), above ground (Sternorrhyncha) or in ground (Cicadomorpha). Probably with the evolution of lignophytes leading to angiosperms that allowed new feeding strategies passing from non-phloem to phloem feeding (CAMPBELL *et al.*, 1994, 1995), each group had the opportunity to radiate independently in an above ground level:



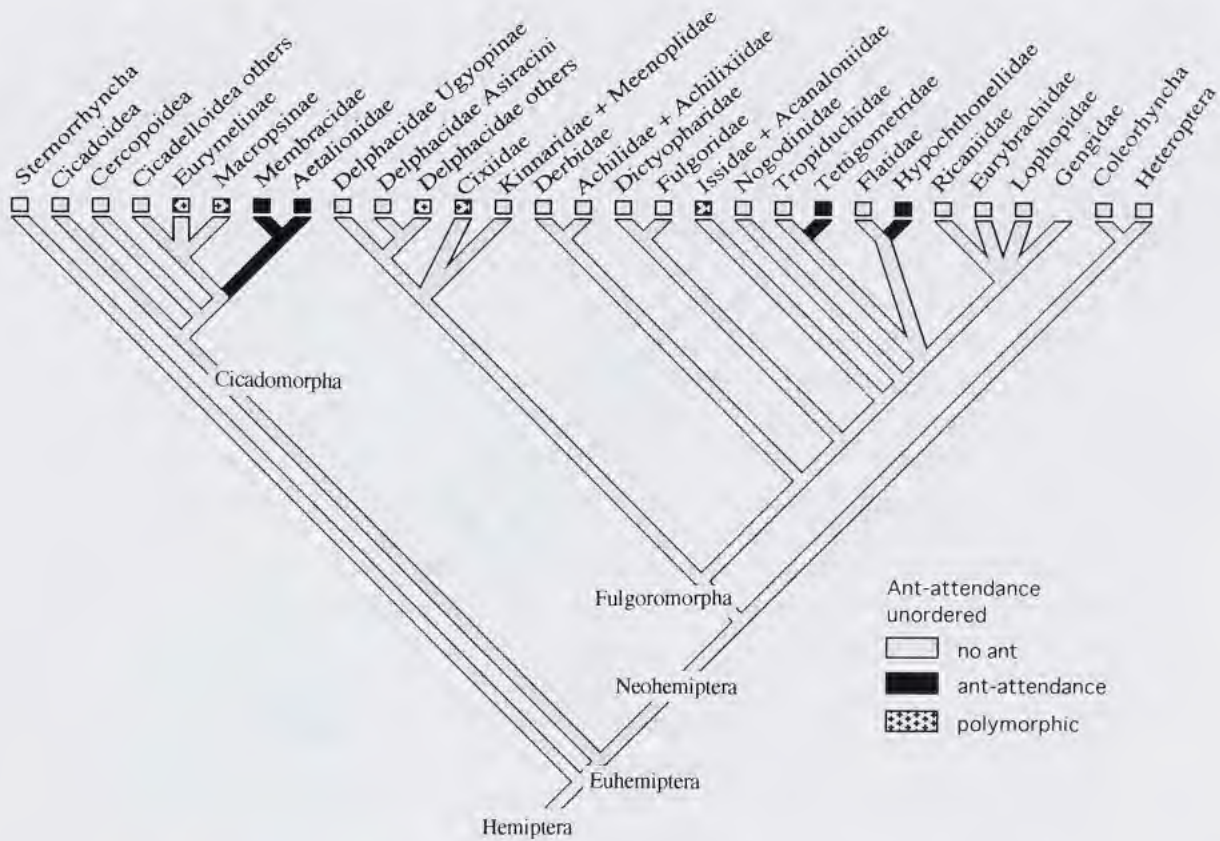


FIG. 3. — Optimization of the ant-attendance attribute upon the phylogeny of the Hemiptera.

recent Sternorrhyncha, Membracoidea, higher Fulgoromorpha and secondary phytophagous Cimicomorpha and Pentatomorpha Heteroptera.

Ant-associations do not appear to be an ancestral condition in Hemiptera. Such a result agrees with the fact that Formicidae is a recent taxon – the oldest known ant fossil is from Upper Cretaceous, 80 millions of years old (HOLLOBLER & WILSON, 1989; BOLTON, 1994) – relatively to Hemiptera which are known since the Permian (see review in SORENSEN *et al.*, 1995). Ant-attendance occurred always after change of the habitat from on ground to above ground and subterranean associations with ants appear to be derived. But not all above ground clades are ant-attended and there is no direct link (causation) between change of habitat and trophobiosis. Probably changes of habitat to an above ground level occurred with changes of host plants. One may expect that host plants mediate Hemiptera attractiveness and that some host plants are more suitable for trophobiosis than others.

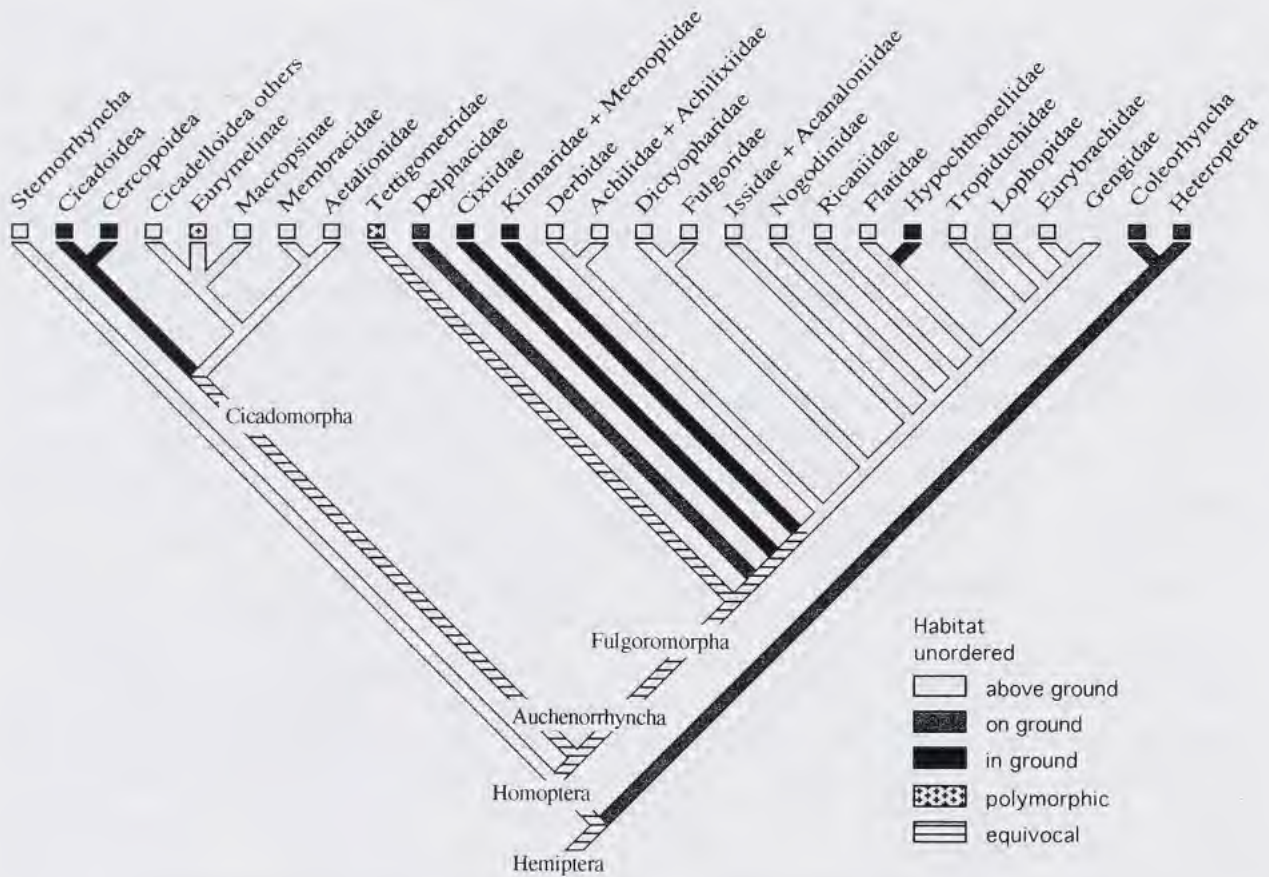


FIG. 4. — Optimization of the habitat attribute (in, on or above ground) upon the phylogeny of the Hemiptera used by SCHAEFER (1987). One cannot choose between the character states for the Hemiptera, the Homoptera, the Auchenorrhyncha, the Cicadomorpha and the Fulgoromorpha.

In Fulgoromorpha, the cixiidian lineage retained the probable ancestral habitat on ground (at least at nymphs) and within this lineage, the Kinnaridae and several Cixiidae taxa went in a subterranean habitat (HOCH, 1994). From the paraphyletic Kinnaridae (BOURGOIN, 1993a) the above ground Meenoplidae family arose. In the sister lineage, the first Derbidae-Achilidae-Achilixiidae lineage specialized as fungal feeders (nymphs) under the bark of living and dead trees (WILSON *et al.*, 1994) while its above ground sister group radiated successfully in number (half of the known species in Fulgoromorpha) and in diversity (13 families). This success is probably related to angiosperm diversification but also with vicariance events linked to the breakup of Gondwana that led to the constrained distributions (absence in some biogeographical areas) observed in some of these families. Within the Fulgoromorpha and with exception of some scattered examples, the Tettigometridae is the only lineage which has developed strong mutualistic relationships with ants. One may expect that radiation of Tettigometridae from Tropiduchidae (BOURGOIN *et al.*, 1997) took place with change of host plants which have influenced their attractiveness to ants either directly (quality of honeydew) or indirectly (plant ant attractants).

*Trophobiosis in Fulgoromorpha and the case of Tettigometridae. Prospectives*

Theoretical studies (ROUGHGARDEN, 1975; WILSON, 1983; KEELER, 1985) suggest that mutualism should be restricted to situations where the cost of maintaining the situation is low to each participant, while the benefits are relatively great (BRISTOW, 1991). Fulgoromorpha-ant associations would seem to fit these restrictions. Indeed, benefits/costs for both partners of such associations are already well known in other Homoptera and are also valid for Fulgoromorpha associations. Ants benefit in reduced search time for food (honeydew) and for prey pursuit by direct predation on the hoppers, and in increased stability and quantity of the food resource. Benefits for the fulgoromorphs include defense against predators which allows a relative perennial site of food and non accumulation of honeydew on the substrate (ROZARIO *et al.*, 1993). Cost for ants includes active defense against predators and active monopolization of fulgoromorphan resources while a higher honeydew production by the hopper is requested.

However among Fulgoromorpha, ant-mutualism is only documented in few species of Cixiidae (MYERS, 1929; THOMPSON, 1984), Delphacidae (DEJEAN *et al.*, 1996), Issidae (DIETRICH & MCKAMEY, 1990), Hypochthonellidae (CHINA & FENNAH, 1952) and in most species of Tettigometridae (BOURGOIN, in prep.). Why are so few Fulgoromorpha ant-attended? Why do more than 70% of the records concern the Tettigometridae? Are there phylogenetic constraints (morphological or behavioral adaptations) which could limit or favor ant-associations and should be hypothesized to account for this pattern? What is the impact of ant-attendance on such adaptations?

Although such generalizations should be approached with some caution (BRISTOW, 1991), regularly ant-attended aphids show several characteristics: *e.g.* cornicle length reduced, leg length reduced, not saltatorial, trophobiotic organ, ... (WAY, 1963; SKINNER, 1980; SUDD, 1987,...) and placid behavior, gregariousness (DIXON, 1958; PIERCE *et al.*, 1987). These characteristics seem to fit with those observed for the Tettigometridae within the Fulgoromorpha. Indeed tettigometrid larvae share several unique morphological characteristics (no jumping apparatus, no wax plates, no sensory pits, a long anal tube, absence of anal combs and anal apodemes in adults) and particular behavioral traits (subsociability, sessile behavior).

*Morphological characteristics.* Considering the function of these structures and correlation with myrmecophily, it appears legitimate to hypothesize an adaptive scenario that these autapomorphic characters in Tettigometridae have evolved under selection for tettigometrid-ant mutualism and thus may be secondarily simplified (versus showing a plesiomorphic state) or lost (versus primary absence). From a phylogenetic standpoint, all these tettigometrid characters have been considered plesiomorphic and homologous to the cicadomorphan state. But, with a new careful and extended morphological analysis (thus independently with regard to this adaptive scenario to avoid circular reasoning), can the primary homology of these characters *a priori* hypothesized with the cicadomorphan state, be rejected? For instance, a new morphological analysis of the characters "long anal tube" and "absence of anal combs" have shown that they are in fact secondarily modified for the first, or reduced or secondarily absent for the second



(BOURGOIN & CAMPBELL, 1996). At least, these two misinterpreted characters may carry an adaptive value for trophobiosis in ant-associations. The other characters need to be reanalyzed according to this possibility.

*Sessile and subsociality behavior.* Four main types of ant-attendance have been reported in Fulgoromorpha literature: 1. Opportunistic or occasional attendance by ants which collect on the substrate the honeydew drops randomly deposited by the planthopper kicking; such associations are generally limited in time (one flatid: PFEIFFER, 1996; some cixiids: O'BRIEN, 1988; DIETRICH & MCKAMEY, 1990). 2. Underground attendance in ant nests (some cixiids: MYERS, 1929; SHEPPARD *et al.*, 1979; THOMPSON *et al.*, 1979; THOMPSON, 1984; hypochthonellids (CHINA & FENNAH, 1952), some tettigometrids). 3. Attendance of planthoppers under shelters build by ants (some delphacids, reviewed in DEJEAN *et al.*, 1996). 4. Long time attendance; ants collect honeydew drops directly at the anal opening and regularly antennate the planthoppers (many tettigometrids, Figs 5-10).

DIETRICH & MCKAMEY (1990) have noted that all ant-attended Membracoidea and Cicadelloidea are sessile (non-jumping) and exhibit subsocial behaviors. It is thus interesting to note that (i) all durable fulgoromorphan-ant associations are observed when planthoppers are either unable to escape (unground in ant galleries or under shelter) or sessile species (Tettigometridae) and (ii) all durable fulgoromorphan-ant associations are observed when planthoppers are either forced into gregariousness (cixiids kept in ant nests, delphacids kept under ant shelters) or when they are subsocial (tettigometrids). Such close correlations are noticeable and further studies are needed to elucidate the relationships between these different attributes: ant-mutualistic, sessile, gregarious and subsocial behaviors.

In Fulgoromorpha, modalities of trophobiosis appear to be quite diverse while it is limited to few species only. Although morphological and behavioral characteristics seem important for mutualistic relationships between planthoppers and ants, one cannot forget that habitat and particularly host plants may have had an important impact on formation and maintenance of these associations. This makes the Fulgoromorpha a nice model to study ant mutualism. Mapping such attributes within a parsimonious evolutionary framework will allow to move from an anecdotal and descriptive natural history to a refutable evolutionary scenario of "how mutualistic interactions evolve and are maintained" (BRISTOW, 1991).

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FIGS 5-10. — **5-9:** *Euphyonarthex phyllostoma* Schmidt (Fulgoromorpha Tettigometridae) attended by various species of ants (Hymenoptera, Formicidae) on *Bridelia micrantha* Baillon (Euphorbiaceae) in Cameroun. **5:** Attended by *Camponotus brutus* Forel; in the upper left part of the photograph one can also observe a dictyopharid (Fulgoromorpha, Dictyopharidae) feeding. **6:** Attended by *Oecophylla longinoda* Latreille (in laboratory). **7:** Attended by *Camponotus acvapimensis* Mayr. **8:** Attended by *Polyrhachis laboriosa* Smith (in laboratory). **9:** Nymphs attended by *Myrmecaria opaciventris* Emery. **10:** *Hilda rubrospersa* Fennah (Fulgoromorpha Tettigometridae) attended by *Camponotus sp.* (*brutus* group) (Hymenoptera, Formicinae) on *Ficus vallis-choudae* Delile (Moraceae), in Cameroun. Photographs by A. DEJEAN.

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